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THE EFFECTS OF TEMPERATURE ON NEST PREDATION BY MAMMALS, BIRDS, AND SNAKES

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Abstract.—Understanding how weather influences survival and reproduction is an important component of forecasting how climate change will influence wildlife population viability. Nest predation is the primary source of reproductive failure for passerine birds and can change in response to temperature. However, it is unclear which predator species are responsible for such patterns because predation events are rarely observed. We investigated whether temperature influenced predator-specific rates of nest predation by analyzing data from six prior studies conducted between 1997 and 2010 in Texas, Illinois, and Missouri that used constant-surveillance video systems to identify predators at the nests of Golden-cheeked Warblers (*Setophaga chrysoparia*), Black-capped Vireos (*Vireo atricapilla*), Indigo Buntings (*Passerina cyanea*), and Acadian Flycatchers (*Empidonax virescens*). Rates of nest predation by snakes and birds increased as daily maximum temperatures increased, whereas predation by mammals was essentially invariant in response to temperature. The relative roles of physiological versus community-level mechanisms (e.g., abundance or behavior of predators and/or alternative prey) in driving the patterns we observed remain unclear, but our data point to the need to consider important biological interactions when forecasting the effects of climate change on songbird populations. *Received 21 February 2013, accepted 27 June 2013.*

Key words: cause-specific mortality, nest survival, passerines, temperature, weather.

Efectos de la Temperatura en la Depredación de nidos por parte de Mamíferos, Aves y Serpientes

Resumen.—Entender cómo el clima afecta la supervivencia y la reproducción es un componente importante para predecir cómo se vería influenciada la viabilidad de las poblaciones silvestres por el cambio climático. La depredación de los nidos es la fuente primaria del fracaso reproductivo en aves paserinas y puede cambiar en respuesta a la temperatura. Sin embargo, no es claro cuáles especies depredadoras son responsables de dichos patrones debido a que los eventos de depredación rara vez son observados. Investigamos si la temperatura afecta las tasas de depredación de nidos específicas para cada depredador mediante el análisis de datos de seis estudios previos conducidos entre 1997 y 2010 en Texas, Illinois y Missouri. Dichos estudios usaron sistemas de monitoreo constante mediante vídeo para identificar depredadores en los nidos de *Setophaga chrysoparia*, *Vireo atricapilla*, *Passerina cyanea* y *Empidonax virescens*. Las tasas de depredación de los nidos por parte de aves y serpientes se incrementaron con aumentos en la temperatura máxima diaria, mientras que la depredación por mamíferos fue esencialmente invariable en relación con la temperatura. Aún no es claro cuál es el papel relativo de los mecanismos fisiológicos o de los mecanismos a nivel de comunidad (e.g., abundancia o comportamiento de los depredadores y/o de las presas alternativas) en la definición de los patrones que observamos, pero nuestros datos apuntan a la necesidad de considerar interacciones biológicas importantes al predecir los efectos del cambio climático en las poblaciones de aves.

Climate change has already had a substantial effect on the flora and fauna of our planet (Parmesan and Yohe 2003). Warmer temperatures associated with climate change often result in birds breeding earlier in the season (Visser et al. 2009), which can lengthen the breeding season and improve productivity (Dunn and Winkler 2010) but can also lead to a mismatch between the phenology of migrating birds and their food resources (Both et al. 2006). Extreme climatic events (e.g., hurricanes and droughts) have increased in frequency in some regions of the world (Easterling et al. 2000), are expected to increase in frequency throughout much of the United States (Karl et al. 2009), and can result in complete reproductive failure or reductions in survival rates of birds (Moreno and Møller 2011). Understanding how facets of climate change influence survival and reproduction is critical if we are to

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accurately forecast how continued climate change will influence the viability of bird populations.

One limiting factor on songbird productivity is nest predation, which is a primary source of reproductive failure (Martin 1992) that can cause low rates of nest survival (e.g., Robinson et al. 1995) and, thus, a demographic parameter that can influence population viability (Donovan and Thompson 2001). Recent work has shown a variable influence of temperature on nest predation risk; predation rates may increase (Cox et al. 2013), decrease (Skagen and Yackel Adams 2012), or not change (Dyrcz and Halupka 2009, Wesołowski and Maziarz 2009) in response to warmer temperatures. Nevertheless, warmer temperatures associated with climate change have the potential to substantially influence songbird demography. For example, a 2–3°C increase in average breeding-season temperature (independent of changes in precipitation) may increase nest survival of Lark Buntings (*Calamospiza melanocorys*) by 31–50% in shortgrass prairie (Skagen and Yackel Adams 2012), whereas period nest survival of Acadian Flycatchers (*Empidonax virescens*) declined from 84% (95% confidence interval [CI]: 0.70–0.93) to 10% (95% CI: 0.04–0.24) across a range of observed breeding-season temperatures in highly forested landscapes of Missouri (Cox et al. 2013).

The variable response of nest survival rates to temperature probably reflects the variation in the predator species primarily responsible for nest failure in different systems. For example, mammals may be more frequent predators in grasslands, snakes may be more frequent predators in forest and shrubland systems (Thompson and Ribic 2012), and nest predation rates by small mammals and Brown-headed Cowbirds (*Molothrus ater*) may increase and decrease, respectively, as regional forest cover increases in the Midwestern United States (Cox et al. 2012b). Because snakes are ectotherms, one may expect systems in which they are dominant nest predators to be more sensitive to temperature changes than ones in which most predators are endotherms. Indeed, snake movement generally increases with warmer temperatures (Peterson et al. 1993), and increased movement may correlate with greater nest predation rates (Sperry et al. 2008, 2012).

There is great benefit to concomitantly investigating the effect of temperature on predator movement and rates of nest predation (e.g., Sperry et al. 2008, 2012), but such an approach does not explicitly link predator movement and nest predation when actual predation events on nests are not recorded. Furthermore, although studying a single predator species or taxon is often all that is logistically feasible, it neglects the fact that there is often a broad suite of predator species contributing to overall predation rates (e.g., Benson et al. 2010, Conner et al. 2010, Reidy and Thompson 2012) and the potential for other species to respond to temperature. For example, endothermic predators may have relatively narrow thermoneutral zones (i.e., the range of temperatures at which an animal does not need to adjust its metabolic rate or behavior to heat or cool itself) and, thus, have increased energetic demands when temperatures are above or below a small range of moderate temperatures. Predators may also have young whose energetic requirements are closely tied to ambient temperatures because they are incapable of thermoregulation (e.g., altricial birds).

Researchers have increasingly used video technology to monitor nests (Cox et al. 2012a), which allows for the identification of nest predators and the estimation of covariate effects on predator-specific rates of nest predation. We combined data from our previous video monitoring studies in old fields and deciduous hardwood forests in Missouri and Illinois, and in scrubland and juniper–oak woodlands in Texas to investigate whether temperature influenced predator-specific rates of predation. Our previous work in Missouri showed that rates of nest predation increase with warmer temperatures for some species in forested landscapes (Cox et al. 2013); we predicted that such a pattern would be related to the correlation between temperature, movement of the Black Rat Snake (*Elaphe obsoleta*; the primary snake predator in our prior studies in all three states), and nest predation rates as found by Sperry et al. (2008). We also investigated the effect of temperature on nest predation rates by other predator groups (e.g., birds, mammals), though the lack of data in the literature precluded us from making predictions on which predators might be influenced by temperature.

Methods

Data collection.—We combined data from six studies that investigated predator-specific rates of nest predation (Stake and Cimprich 2003; Thompson and Burhans 2003; Stake et al. 2004; Reidy et al. 2008, 2012; Cox et al. 2012c) at two sites in Texas, four sites in Illinois, and four sites in Missouri (Fig. 1). Sites in Texas were characterized by juniper–oak (*Juniperus ashei* and *Quercus* spp.) woodlands and scrublands. Sites in Missouri and Illinois were characterized by mid- to late-successional deciduous forests dominated by oaks and hickories (*Carya* spp.). Forest openings included old fields, food plots, power lines, and pastures. Cowbird control measures were in place at one of the sites in Texas; no predator control measures were in place at any other site.

We restricted this study to four species from our prior studies with the greatest sample sizes. In Texas, our study focused on two federally endangered Neotropical migrant songbirds, the canopy-nesting Golden-cheeked Warbler (*Setophaga chrysoparia*; hereafter "warbler") and the shrub-nesting Black-capped Vireo (*Vireo atricapilla*; hereafter "vireo"). Previous work estimated period nest survival to be 40% for warblers (Reidy et al. 2009) and 26% for vireos (Bailey 2005). The two focal species in Missouri and Illinois were the Acadian Flycatcher (hereafter "flycatcher"), a migrant forest-interior species that typically nests in the subcanopy, and the Indigo Bunting (*Passerina cyanea*; hereafter "bunting"), a migrant species that nests in shrubs in old fields, forest edges, and the forest interior where the understory vegetation is adequately dense. Nest survival rates at our study sites were substantially lower for buntings (19%) than for flycatchers (42%) (W. A. Cox unpubl. data).

Nest-searching and video-monitoring protocols were determined by the original researchers (Stake and Cimprich 2003, Thompson and Burhans 2003, Stake et al. 2004, Reidy et al. 2008, Cox et al. 2012c) but were similar because all studies were affiliated with the same research group. Briefly, nests were found via systematic search and by using cues from parental behavior. Cameras were camouflaged to reduce the chance of influencing adult or predator behavior and were placed 0.3–4.5 m from the nest, depending on the camera type and species. In most cases, to reduce the risk of abandonment, cameras were not placed at a nest until after the final egg of a clutch was laid. Cameras were connected by cable to videocassette or digital video recorders, which

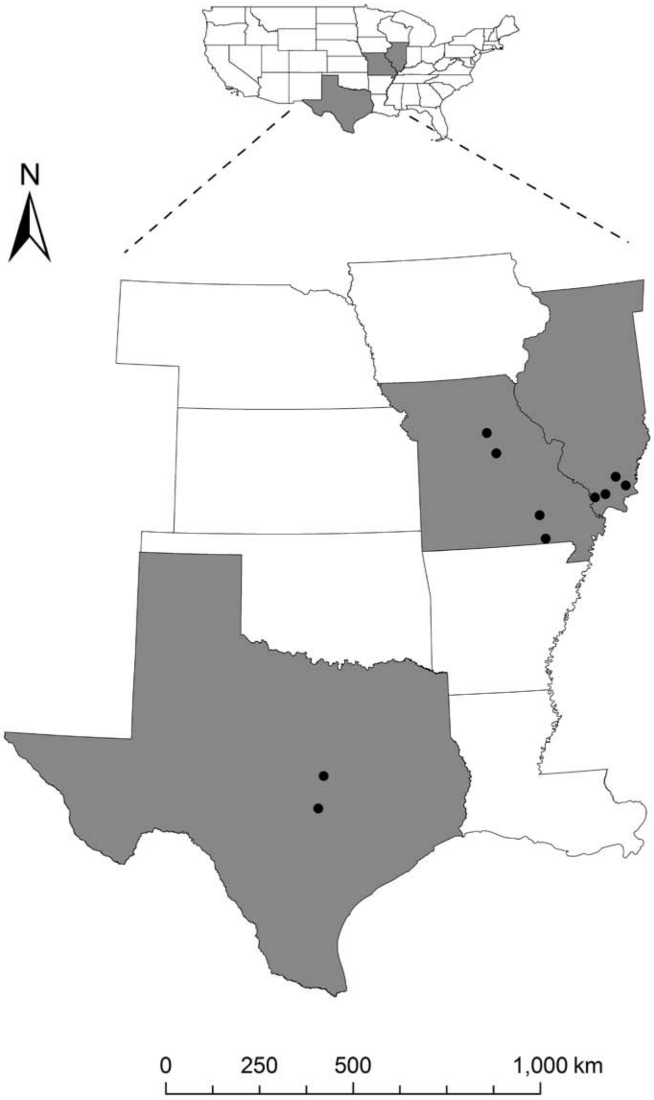

Fig. 1. Sites in Texas, Missouri, and Illinois from six studies that used video-monitoring to identify nest predators at various times during 1997–2010.

were placed in weather-proof cases about 10–15 m from the nest to avoid disturbing nests when batteries and media were changed (at intervals of 1–3 days). Videos were reviewed when nest contents changed between nest-monitoring intervals, and researchers identified predators to the lowest possible taxon.

We obtained maximum daily temperature data from the Midwest Regional Climate Center and the National Oceanic and Atmospheric Administration National Climatic Data Center (see Acknowledgments). We identified the weather stations nearest to nests using ARCMAP, version 9.3 (ESRI, Redlands, California). The mean distance from each nest ($n = 649$) to the nearest weather station ($n = 10$) was 14.5 ± 0.2 km (range: 5.3–27.3 km).

Analysis.—We used multinomial logistic regression within an information-theoretic approach (Burnham and Anderson 2002) to evaluate the relative support for candidate models that represented hypotheses of factors potentially influencing predator-specific rates of nest predation. The use of multinomial logistic regression is similar to traditional nest-survival analyses (e.g., logistic exposure; Shaffer 2004) in that nest-monitoring intervals are the sampling unit and covariates can be interval, nest, or site-specific. However, the approach differs from nest survival analyses in three ways. First, a link function that incorporates the length of the nest-monitoring interval is not required because intervals from video-monitoring data represent each 24-h period that a nest is monitored, so predicted probabilities of events represent daily rates without any adjustment. Second, we treated partial predation as a predation event, whereas an interval during which ≥1 egg or nestling is present is typically considered successful in nest survival analyses. Third, the multinomial model allows multiple response levels rather than the binary response (success or failure) used in nest survival models. Small sample sizes precluded the use of species-specific response levels, so we grouped predators and used four response levels (1 = mammal, 2 = bird, 3 = snake, 4 = survived or other). The fourth response level indicated a successful interval, one with an unknown fate (e.g., because of camera failure), or one during which a nest failed from causes other than mammals, birds, or snakes (e.g., weather, nest abandonment, ant predation; for details on the frequency of these sources of nest failure, see Cox et al. 2012c, Reidy and Thompson 2012). We treated failed predator attacks (e.g., premature forced-fledging events or predator visits after which the nest contents remained unchanged) as a successful interval. To reduce concerns about pseudoreplication, only the first successful attack on a nest by a particular predator species was treated as a predation event (multiple predation events on a nest were still coded as such if different species were responsible, however). Our results are not directly comparable to typical nest survival rates because we are predicting the probability of three specific responses (events), which are not analogous to the traditional definition of nest successes.

Because of small sample sizes of some predator group–focal species combinations, we decided *a priori* to minimize the number of covariates we included in candidate models. We also decided to maximize the power of our data set by running a unified analysis with species as a covariate rather than run each species separately. We addressed the possibility that regional effects (e.g., Texas vs. Missouri–Illinois) could overwhelm species effects because of the differences in habitat type, climate, and predator species between the two regions by including each basic model twice in the candidate set, once with a species covariate and once with a region covariate. The simplest model included a species–region term, a term for nest stage (incubation vs. nestling period) because of the strong age and stage effects noted in our previous work (Cox et al. 2012c, Reidy and Thompson 2012), and a term for date to isolate the effect of temperature from other seasonal factors that could influence patterns of nest predation. A preliminary analysis indicated a lack of strong multicollinearity between the temperature and ordinal date (tolerance value for all data: 0.92; for Texas data: 0.69; for Missouri–Illinois data: 0.96; Allison 1999), which allowed us to include both variables in all models. We assessed models with linear and quadratic effects of temperature because, although snake movement increases with temperature, snakes may avoid activity during the hottest temperatures when locomotor performance of ectotherms can decline substantially near critically high temperatures (Bennett 1990). We included a model with a nest stage * temperature interaction because some predators, including snakes, are substantially more likely to depredate nests during the nestling stage (Cox et al. 2012c, Reidy and Thompson 2012). Treating species–region as a covariate in an additive model produces a separate intercept for each species–region but assumes that the slope of a temperature effect is consistent across species–regions. To allow for the possibility of species- or region-specific responses to temperature, we also included models with a species–region * temperature interaction. Finally, we included a global model. We ranked models using Akaike's information criterion (AIC) and calculated Akaike weights (w_i) for each model, which represent the relative strength of support for a given model when compared to all other models in the candidate set. Model averaging parameters is problematic when terms are involved in interactions in some models but not others (Burnham and Anderson 2002), so we present model-averaged predictions across the suite of candidate models to account for uncertainty in the model selection process. We ran all models in SAS, version 9.2 (SAS Institute, Cary, North Carolina), using PROC GLIMMIX. Results are presented as means ± SE unless otherwise noted.

RESULTS

Our data set included 649 nests (193 buntings, 177 flycatchers, 149 warblers, and 130 vireos) that were video-monitored during 1997–2010 for a total of 7,229 observation days. Mammals depredated ≥1 egg or nestling on 38 observation days, birds depredated ≥1 egg or nestling on 113 observation days, and snakes depredated ≥1 egg or nestling on 83 observation days (61 of 71 snakes identified to species [86%] were Black Rat Snakes). Nests were successful or lost eggs or young to other causes on the remaining observation days ($n = 6{,}995$). Overall mean maximum daily temperature was 30.2 ± 0.04°C (range: 14.4–42.8°C); means were similar in both study areas (Missouri–Illinois: 30.3 ± 0.05°C, range: 15.0–39.4°C; Texas: 30.2 ± 0.08°C, range: 14.4–42.8°C) because the breeding season was earlier for warblers and vireos (median observation day: 9 May; range: 1 April–27 July) than for buntings and flycatchers (median observation day: 27 June; range: 20 May–13 August).

All models with the species variable were supported over those with region (Table 1). The top model included species, nest stage, temperature, and date. Temperature was included as an additive term in two of the top three models, which accounted for 63% of the total model weight. Models with interaction terms between temperature and species or nest stage were not well supported. Model-averaged predictions of predator-specific predation rates as a function of temperature indicated that nest predation by birds and snakes exhibited a similarly positive response to temperature, with predation increasing by 48% and 70% for birds and snakes, respectively, between the 5th and 95th percentiles of observed temperatures (Fig. 2A). The effect of temperature leveled off at extremely hot temperatures, with daily predation rates between 37.2°C (birds: 0.0138; [95% CI: 0.0081–0.0233], snakes: 0.0106 [95% CI: 0.0057–0.0197]) and 42.8°C (birds: 0.0140 [95% CI: 0.0045–0.0428], snakes: 0.0113 [95% CI: 0.0030–0.0409]) increasing by just 1% and 6% for birds and snakes, respectively. However, confidence intervals were wide because of small sample sizes at extreme temperatures. By contrast, mammals exhibited a relatively invariant response to temperature, with a small increase in predation rates occurring at moderate temperatures (Fig. 2A).

Table 1. Support for models representing hypotheses of species, region, temporal, and temperature effects on predator-specific rates of nest predation for Indigo Buntings and Acadian Flycatchers in Missouri and Illinois and for Golden-cheeked Warblers and Black-capped Vireos in Texas, 1997–2010.

Model	*K*	AIC	ΔAIC	w_i
Species + nest stage + maxtemp + date	21	2,485.04	0.00	0.39
Species + nest stage + date	18	2,485.44	0.40	0.32
Species + nest stage + maxtemp^2 + date	24	2,486.01	0.97	0.24
Species + (nest stage * maxtemp) + date	24	2,489.73	4.69	0.04
(Species * maxtemp) + nest stage + date	30	2,493.04	8.00	0.01
(Species * maxtemp) + (nest stage * maxtemp) + date	33	2,497.63	12.59	0.00
Region + nest stage + date	12	2,504.91	19.87	0.00
Region + nest stage + maxtemp + date	15	2,505.31	20.27	0.00
Region + nest stage + maxtemp^2 + date	18	2,506.57	21.53	0.00
(Region * maxtemp) + nest stage + date	18	2,508.84	23.80	0.00
Region + (nest stage * maxtemp) + date	18	2,509.73	24.69	0.00
(Region * maxtemp) + (nest stage * maxtemp) + date	21	2,513.26	28.22	0.00

When assessing support for models with multinomial response variables within an information-theoretic framework, each additional parameter must overcome a 2-point AIC penalty for each level of the response variable (e.g., with three response levels, the AIC penalty for each covariate is 6 points). As such, support for a particular model may not be strong if a subset of the response levels is not well represented by the model. We therefore performed a post hoc analysis of our candidate models in which we grouped predation by mammals with the reference level to assess the relative strength of the models when only predation by birds and snakes was considered. Here, the top two models included a linear (AIC = 2,005.62, $w_i = 0.49$) and a quadratic (AIC = 2,007.60, $w_i = 0.18$, ΔAIC = 1.98) term for temperature, respectively, and accounted for 67% of the overall weight. The null was the third-ranked model (AIC = 2,007.63, $w_i = 0.18$, ΔAIC = 2.01) and accounted for 18% of the model weight.

Although we lacked the sample sizes necessary to conduct a full analysis of each focal bird species separately, we performed a second post hoc analysis and fit an additive model with nest stage, temperature, and date for each species to see whether temperature effects were consistent with the most supported model in the pooled analysis. As we expected, standard errors for the temperature coefficients were large because of smaller sample sizes, and 95% confidence intervals overlapped zero for all but snake predation on warbler nests. However, temperature coefficients were positive for both bird and snake predation on flycatchers, buntings, and warblers, and therefore consistent for three of four species with the pooled analysis. Temperature and mammal predation were negatively related for flycatchers, buntings, and vireos, but positively and more strongly related for

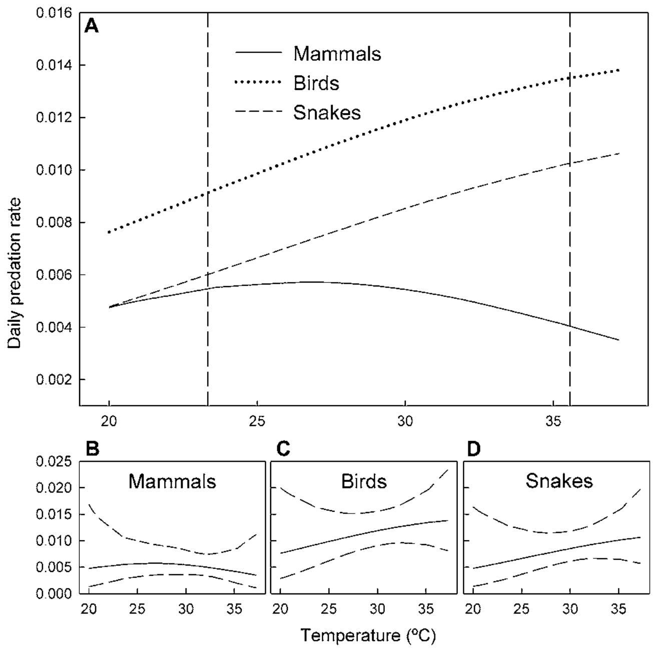

Fig. 2. Model-averaged predicted estimates of nest predation as a function of maximum daily temperature by mammals, birds, and snakes. Estimates are for a hypothetical population of birds balanced across the four focal species because model-selection results did not support focal species-specific slopes of the temperature effect. Estimates are also balanced across the incubation and nestling stages and are for the mean ordinal date (161) of our sample. Estimates are presented for the 2.5th–97.5th percentiles of observed temperatures, with vertical dashed lines in panel A representing the 5th and 95th percentiles of observed temperatures. Estimates in B–D include associated 95% confidence intervals.

warblers, which likely offset the negative effect for the other species and explains the lack of an effect of mammal predation in the pooled analysis.

DISCUSSION

Scientists have expended considerable effort to understand the importance of nest predation with respect to the ecology, evolution, and conservation of birds. However, the difficulty of identifying nest predators has often left us with an incomplete understanding of the mechanisms responsible for observed patterns of nest predation. Here, we investigated predator-specific rates of nest predation with respect to daily temperatures in an attempt to better understand why birds might experience changed rates of reproductive success as temperatures increase (e.g., Skagen and Yackel Adams 2012, Cox et al. 2013). Predicted nest predation by snakes and birds increased with warmer temperatures, whereas it remained relatively invariant for mammalian predators. We acknowledge that there was considerable uncertainty surrounding predicted probabilities of predation for all three predator groups at the highest and lowest observed temperatures (Fig. 2B–D), and we suggest a cautious interpretation of the observed patterns. Nevertheless, our results offer insight into how predator–prey interactions may be influenced by temperature and provide a starting point for understanding how climate change may influence the productivity of the focal species.

The association between increased temperatures and increased predation by snakes is likely related to the thermal biology of snakes. Many ectothermic species exhibit increased metabolic rates and increased locomotion with increased temperatures, albeit with a decline in locomotor ability and movement at temperatures near lethal levels (Bennett 1990). In addition to more rapid movement, snakes also exhibit improved locomotor performance (e.g., they fall less frequently) in arboreal environments as temperatures increase (Gerald et al. 2008). It seems reasonable that increased energetic requirements coupled with increased movements and improved locomotor performance would result in greater rates of predation by snakes on songbird nests during warmer weather. Furthermore, this effect began to plateau at ~35°C, which is consistent with the preference of most snake species for ambient temperatures of 28–34°C (Lillywhite 1987) and their tendency to avoid activity during the hottest temperatures (Weatherhead et al. 2012). However, it is important to note that although our post hoc analyses indicated that predation by snakes was associated with increased temperatures for Golden-cheeked Warblers but not Black-capped Vireos, Sperry et al. (2008) found that snake movement was correlated with vireo nest survival and uncorrelated with warbler nest survival. Studies that simultaneously track predators and predator-specific nest predation across a temperature gradient are needed to better our understanding of temperature effects on nest predation.

The mechanisms by which temperature influenced rates of predation by birds are less clear. At temperatures greater than their thermoneutral maxima, endotherms may exhibit increased metabolic rates and increased energetic expenditures associated with panting and other heat-reduction behaviors (Cossins and Bowler 1987), which could increase daily energetic requirements for predator species (and, thus, rates of nest predation). However, there are few published data on the thermoneutral zones of the species that frequently depredated nests in the present study, so it is difficult to assess how important a role the thermoneutral maxima of predator species play in contributing to patterns of predation by birds. It is also unclear why this might influence predation by endothermic birds but not by mammals, predation by which was essentially independent of temperature. Quantification of thermoneutral zones for a wide range of species will help clarify whether these factors are important determinants of predator-specific rates of predation on songbird nests.

It is possible that temperature indirectly influenced predation rates by altering parental behavior at the nest. If high temperatures increased the energetic needs of nestling songbirds (which are incapable of thermoregulation during the first portion of their lives), parent birds might respond with increased nest visitation rates, which can increase rates of predation (Martin et al. 2000). This could, in part, explain the divergence in temperature effects on avian and mammalian predators. Predation by birds almost always occurred during the day (109 of 113 events; 96%) by diurnal, visually oriented species (e.g., corvids, cowbirds, and Broad-winged Hawks [*Buteo platypterus*]), as well as species typically thought of as nocturnal; only 1 of 8 (13%) predation events by Barred Owls (*Strix varia*) occurred at night. Predation by mammals (e.g., Fox Squirrels [*Sciurus niger*] and Gray Foxes

[*Urocyon cinereoargenteus*]) also usually occurred during the day in Texas (11 of 14 events; 79%), but predation by mammals in Missouri and Illinois (e.g., rodents and Raccoons [*Procyon lotor*]) occurred almost exclusively at night (22 of 23 events; 96%), which could reduce the strength of a linkage between adult songbird behavior and nest predation by mammals. It is unclear whether adult behavior could influence the risk of predation by snakes because, although much of the snake predation occurred at night (38 of 44 events in Texas [86%]; 12 of 38 events in Missouri–Illinois [32%]), many snakes are thought to be visually oriented nest predators (Weatherhead and Blouin-Demers 2004), and some researchers have proposed that snakes locate nests during the day but depredate them at night when the thermal environment is more conducive to movement (Stake et al. 2005).

Nest predators do not exist in isolation from one another, and it is possible that patterns of predator-specific nest predation are driven in part by interactions between the predator species. For example, 26 of 38 predation events (68%) by mammals were caused by relatively small species (e.g., sciurids and mice) that may also be preyed upon by raptors and snakes. Though we are not aware of published data on the matter, one can surmise that the abundance or activity of small mammals may change in response to the risk of predation from increasingly active snakes and raptors as temperatures rise. Furthermore, predators of songbird nests are typically generalists that rely on other food sources in addition to eggs and nestlings throughout the breeding season (e.g., Fitch 1963, Goodrich et al. 1996, Tarvin and Woolfenden 1999). Warmer temperatures may influence the availability of alterative prey, which could in turn influence rates of predation on songbird nests.

The diversity of potential mechanisms driving predator-specific changes in nest predation in response to temperature, coupled with the potential for species- and system-specific relationships between temperature and nest predation, highlight the challenges of predicting how continued climate change will influence songbird productivity. We have demonstrated that temperature can influence predator-specific rates of nest predation, but we do not know the degree to which songbirds can adjust either behaviorally or evolutionarily to such changes in predator activity. To our knowledge, there are relatively few data that describe how climatic factors influence the physiology and behavior of the nest-predator species in these systems. We do not know how climate change will influence the distribution or abundance of the suite of predators responsible for nest failure at our sites or how such changes will alter interactions between nest predators and their other prey (some of which may also prey upon songbird nests). Furthermore, only recently have we begun to understand how nest predator–prey interactions vary spatially or between nesting guilds within a habitat patch. Such data are needed because predictive models are most powerful when they incorporate important biological interactions such as those between predators and prey (Van der Putten et al. 2010). Songbird eggs and young are but one resource within complex trophic webs; we will be best positioned to accurately forecast the influence of climate change on avian demographics if we concomitantly consider the community of plants and animals with which they reside.

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Literature Cited

Allison, P. D. 1999. Logistic Regression Using the SAS System: Theory and Application. SAS Institute, Cary, North Carolina.

Bailey, J. W. 2005. Hierarchical nest-site selection and the effects of habitat characteristics on Black-capped Vireo nest survival. M.S. thesis, University of Missouri, Columbia.

Bennett, A. F. 1990. Thermal dependence of locomotor capacity. American Journal of Physiology 259:R253–R258.

Benson, T. J., J. D. Brown, and J. C. Bednarz. 2010. Identifying predators clarifies predictors of nest success in a temperate passerine. Journal of Animal Ecology 79:225–234.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81–83.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York.

Conner, L. M., J. C. Rutledge, and L. L. Smith. 2010. Effects of mesopredators on nest survival of shrub-nesting songbirds. Journal of Wildlife Management 74:73–80.

Cossins, A. R., and K. Bowler. 1987. Temperature Biology of Animals. Chapman and Hall, London.

Cox, W. A., M. S. Pruett, T. J. Benson, S. J. Chiavacci, and F. R. Thompson III. 2012a. Development of camera technology for monitoring nests. Pages 185–210 *in* Video Surveillance of Nesting Birds (C. A. Ribic, F. R. Thompson III, and P. J. Pietz, Eds.). Studies in Avian Biology, no. 43.

Cox, W. A., F. R. Thompson III, and J. Faaborg. 2012b. Landscape forest cover and edge effects on songbird nest predation vary by nest predator. Landscape Ecology 27:659–669.

Cox, W. A., F. R. Thompson III, and J. Faaborg. 2012c. Species and temporal factors affect predator-specific rates of nest predation for forest songbirds in the Midwest. Auk 129:147–155.

Cox, W. A., F. R. Thompson III, J. L. Reidy, and J. Faaborg. 2013. Temperature can interact with landscape factors to affect songbird productivity. Global Change Biology 19:1064–1074.

Donovan, T. M., and F. R. Thompson III. 2001. Modeling the ecological trap hypothesis: A habitat and demographic analysis for migrant songbirds. Ecological Applications 11:871–882.

Dunn, P. O., and D. W. Winkler. 2010. Effects of climate change on timing of breeding and reproductive success in birds. Pages 113–128 *in* Effects of Climate Change on Birds (A. P. Møller, W. Fiedler, and P. Berthold, Eds.) Oxford University Press, Oxford, United Kingdom.

Dyrcz, A., and L. Halupka. 2009. The response of the Great Reed Warbler *Acrocephalus arundinaceus* to climate change. Journal of Ornithology 150:39–44.

Easterling, D. R., J. L. Evans, P. Y. Groisman, T. R. Karl, K. E. Kunkel, and P. Ambenje. 2000. Observed variability and trends in extreme climate events: A brief review. Bulletin of the American Meteorological Society 81:417–425.

Fitch, H. S. 1963. Natural history of the black rat snake (*Elaphe o. obsoleta*) in Kansas. Copeia 1963:649–658.

Gerald, G. W., M. J. Mackey, and D. L. Claussen. 2008. Effects of temperature and perch diameter on arboreal locomotion in the snake *Elaphe guttata*. Journal of Experimental Zoology A 309:147–156.

Goodrich, L. J., S. C. Crocoll, and S. E. Senner. 1996. Broad-winged Hawk (*Buteo platypterus*). *In* The Birds of North America, no. 218 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Karl, T. R., J. M. Melillo, and T. C. Peterson, Eds. 2009. Global Climate Change Impacts in the United States. Cambridge University Press, New York.

Lillywhite, H. B. 1987. Temperature, energetics, and physiological ecology. Pages 422–477 *in* Snakes: Ecology and Evolutionary Biology (R. A. Seigel, J. T. Collins, and S. S. Novak, Eds.). McGraw-Hill, New York.

Martin, T. E. 1992. Breeding productivity considerations: What are the appropriate habitat features for management? Pages 455–473 *in* Ecology and Conservation of Neotropical Migrant Landbirds (J. M. Hagan III and D. W. Johnston, Eds.) Smithsonian Institution Press, Washington, D.C.

Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine. 2000. Parental care and clutch sizes in North and South American birds. Science 287:1482–1485.

Moreno, J., and A. P. Møller. 2011. Extreme climatic events in relation to global change and their impact on life histories. Current Zoology 57:375–389.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Peterson, C. R., A. R. Gibson, and M. E. Dorcas. 1993. Snake thermal ecology: The causes and consequences of body-temperature variation. Pages 241–314 *in* Snakes: Ecology and Behavior (R. A. Seigel and J. T. Collins, Eds.). McGraw-Hill, New York.

Reidy, J. L., M. M. Stake, and F. R. Thompson III. 2008. Golden-cheeked Warbler nest mortality and predators in urban and rural landscapes. Condor 110:458–466.

Reidy, J. L., and F. R. Thompson III. 2012. Predator identity can explain nest predation patterns. Pages 135–148 *in* Video Surveillance of Nesting Birds (C. A. Ribic, F. R. Thompson III, and P. J. Pietz, Eds.). Studies in Avian Biology, no. 43.

Reidy, J. L., F. R. Thompson III, and R. G. Peak. 2009. Factors affecting Golden-cheeked Warbler nest survival in urban and rural landscapes. Journal of Wildlife Management 73:407–413.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.

Skagen, S. K., and A. A. Yackel Adams. 2012. Weather effects on avian breeding performance and implications of climate change. Ecological Applications 22:1131–1145.

Sperry, J. H., D. G. Barron, and P. J. Weatherhead. 2012. Snake behavior and seasonal variation in nest survival of Northern Cardinals *Cardinalis cardinalis*. Journal of Avian Biology 43:496–502.

Sperry, J. H., R. G. Peak, D. A. Cimprich, and P. J. Weatherhead. 2008. Snake activity affects seasonal variation in nest predation risk for birds. Journal of Avian Biology 39:379–383.

Stake, M. M., and D. A. Cimprich. 2003. Using video to monitor predation at Black-capped Vireo nests. Condor 105:348–357.

Stake, M. M., J. Faaborg, and F. R. Thompson III. 2004. Video identification of predators at Golden-cheeked Warbler nests. Journal of Field Ornithology 75:337–344.

Stake, M. M., F. R. Thompson III, J. Faaborg, and D. E. Burhans. 2005. Patterns of snake predation at songbird nests in Missouri and Texas. Journal of Herpetology 39:215–222.

Tarvin, K. A., and G. E. Woolfenden. 1999. Blue Jay (*Cyanocitta cristata*). *In* The Birds of North America, no. 469 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.

Thompson, F. R., III, and D. E. Burhans. 2003. Predation of songbird nests differs by predator and between field and forest habitats. Journal of Wildlife Management 67:408–416.

Thompson, F. R., III, and C. A. Ribic. 2012. Conservation implications when the nest predators are known. Pages 23–33 *in* Video Surveillance of Nesting Birds (C. A. Ribic, F. R. Thompson III, and P. J. Pietz, Eds.). Studies in Avian Biology, no. 43.

Van der Putten, W. H., M. Macel, and M. E. Visser. 2010. Predicting species distribution and abundance responses to climate change: Why it is essential to include biotic interactions across trophic levels. Philosophical Transactions of the Royal Society of London, Series B 365:2025–2034.

Visser, M. E., L. J. M. Holleman, and S. P. Caro. 2009. Temperature has a causal effect on avian timing of reproduction. Proceedings of the Royal Society of London, Series B 276:2323–2331.

Weatherhead, P. J., and G. Blouin-Demers. 2004. Understanding avian nest predation: Why ornithologists should study snakes. Journal of Avian Biology 35:185–190.

Weatherhead, P. J., J. H. Sperry, G. L. F. Carfagno, and G. Blouin-Demers. 2012. Latitudinal variation in thermal ecology of North American ratsnakes and its implications for the effect of climate warming on snakes. Journal of Thermal Biology 37:273–281.

Wesołowski, T., and M. Maziarz. 2009. Changes in breeding phenology and performance of Wood Warblers *Phylloscopus sibilatrix* in a primeval forest: A thirty-year perspective. Acta Ornithologica 44:69–80.

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